

Canopy gap characteristics and disturbance dynamics in old-growth *Picea abies* stands in northern Fennoscandia: Is the forest in quasi-equilibrium?

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Emulating natural disturbances in managed forests has been suggested as a potential solution to maintain habitat conditions similar to those observed in old-growth forests. We examined the gap attributes and disturbance history of old-growth *Picea abies*-dominated stands in the northern boreal vegetation zone of the Pallas-Yllästunturi National Park in northwestern Finland to evaluate the influence of gaps on forest dynamics and the temporal patterns of gap creation. Six stands located at two sites were sampled along 400-m-long linear transects so that all intersected gaps were measured and dated. The average proportion of the forest area in the gaps was $43.1\% \pm 7.5\%$. An average gap size was estimated to be $221 \text{ m}^2 \pm 198 \text{ m}^2$, whereas the median gap size was 170.2 m^2 . While only 20% of the gaps were smaller than 100 m^2 , nearly 85% of them were smaller than 300 m^2 . Gap creation was constant with no distinct peaks from 1965 to 2005. Thus, forest dynamics were driven by continuous small-scale disturbances and were characterized by quasi-equilibrium structure. However, the results of the growth release analysis indicated that more severe disturbance(s) may have occurred almost two centuries ago. Emulating this type of forest dynamics would imply selective or group harvesting of trees as the predominant methods, but larger-scale, more intensive cuttings could also be carried out periodically.

Key words: boreal forest, dendroecology, Finland, gap dynamics, growth release, natural disturbance, stand dynamics

Introduction

In parts of the boreal forest, the prevalence of large-scale severe fire disturbances has led to the view that landscapes are composed of mosaics of even-aged stands (Johnson 1992). However, more recently it has been recognised that in some parts of the boreal forest, the period between fires may far exceed tree longevity. As the fire rotation lengthens, a greater proportion of stands will be affected by gap dynamics (Liu & Hytteborn 1991, Kuuluvainen 1994, Drobyshev 1999, McCarthy 2001, Pham *et al.* 2004). Gap dynamics lead to the development of heterogeneous old-growth characteristics, including an uneven-aged stand structure with a variety of tree size classes and an accumulation of coarse woody debris (Harmon *et al.* 1986, Franklin *et al.* 1987, Oliver & Larson 1996, Mosseler *et al.* 2003).

In the Fennoscandian boreal zone, only fragments of the original old-growth forests remain due to intensive forest management (Esseen *et al.* 1997, Östlund *et al.* 1997). This modification of the forest structure has been identified as a major reason for the decline in biodiversity and the increase in the number of endangered species in the Fennoscandian flora and fauna (Bernes 1994, Rassi *et al.* 2001, Svensson & Jeglum 2001). Protected areas are central to the conservation of threatened species, but these are mainly located in northern areas (Angelstam & Andersson 2001). Ecosystem management and restoration are therefore important complements to ensure the maintenance of biodiversity in regions where managed forests cover most of the landscape. There is a need to gain a better understanding of the characteristics of natural boreal forests in order to develop strategies that will ensure the continuity of such characteristics in managed areas.

In tropical and temperate ecosystems, old-growth forests can be in relative structural and compositional equilibrium, i.e. quasi-equilibrium (Shugart 1984), generated by relatively small, continuous disturbances (Brokaw 1985, Denslow 1985, Runkle 1985b). In other old-growth forest ecosystems, particularly in northern boreal coniferous forests, periodic, synchronous high or moderately severe disturbances, such as insect outbreaks or windthrows, often lead to non-equilibrium

stand dynamics (Sirén 1955, MacLean 1980, Battles & Fahey 2000). However, other studies have suggested that quasi-equilibrium conditions can occur in old-growth boreal forests (Sernander 1936, Kuuluvainen 1994). In general, there is a lack of knowledge on the temporal stability of boreal forest structure and composition under gap disturbance regimes in Fennoscandian forests. Potential earlier insights for Scandinavian boreal forests are inconclusive due to inconsistent mortality-rate estimates (Hytteborn *et al.* 1991, Linder 1998, Fraver *et al.* 2008).

In this study, we examined gap size distribution and disturbance history in old-growth *Picea abies*-dominated stands in northwestern Finland using dendrochronological disturbance reconstruction. We expected low variation in gap sizes as well as in the number of gapmakers per gap, and constant gap creation through time such that the forest would be in a state of quasi-equilibrium (Shugart 1984). The specific study questions were the following: (1) Is gap creation a continuous and steady process or is it characterized by punctual tree mortality events? (2) Is there any evidence of larger scale disturbances playing a role in stand dynamics in addition to gap dynamics?

Methods

Study area

The study area was located in the northern Fennoscandian boreal vegetation zone, in the Pallas-Yllästunturi National Park in northwestern Finland (67°30'–67°44'N, 24°00'–24°55'E). Due to past forest use, only a few old-growth *P. abies* stands remain in this area (Fig. 1). The northern location of the Pallas-Yllästunturi National Park limits the growing season to 100 to 140 days. Mean annual temperature is around –0.8 °C, and the annual amount of precipitation is about 500 mm, with 45% of it falling as snow (Varmola *et al.* 2004). The park encompasses many lakes and is surrounded by rocky mounts, with the highest peak, Pallas, culminating at 807 m. The park has been protected by the Finnish government since the mid-1930s. Forestry activities took place in earlier periods in parts of the park;

however, our study sites both within and outside the park's limits showed no signs of previous logging activities.

Soils in this area originate from glacial till and tend to podzolize easily, which promotes the accumulation of raw humus on the most mesic sites (Sirén 1955, Bonan & Shugart 1989), giving rise to the *Hylocomium–Myrtillus* forest type *sensu* Cajander (1926). The high moisture associated with the *Hylocomium–Myrtillus* forest favours the establishment of *Picea abies* in late successional stages. *Picea abies* is the dominant tree species, followed by *Betula pubescens* and, to a lesser extent, *Pinus sylvestris* (Norokorpi 1979, Esseen *et al.* 1997). The shrub layer includes *Sorbus aucuparia* and *Salix caprea*, while the dwarf-shrub layer is dominated by both *Vaccinium vitis-idaea* and *V. myrtillus* (Esseen *et al.* 1997).

Sampling and measurements

Six *P. abies*-dominated forest sites within the Pallas-Yllästunturi National Park were chosen for this study based on the following criteria: (1) forests growing on the *Hylocomium–Myrtillus* site type, (2) relatively flat topography, and (3) no signs of human impact or recent severe disturbance. Four sites were located in the Pyhäjärvi area (67°46'60"N, 24°13'00"E), and two were in the Pallasjärvi sector (68°1'60"N, 24°11'60"E). The two sectors are about 150 km apart.

To estimate gap characteristics within each site, a 400-m-long linear transect was established in a random direction constrained by the fact that it had to fit into the limits of the stand. The line intersect method has been commonly used in gap studies in boreal forests to measure gap fraction and gap size (e.g. Liu & Hytteborn 1991, Kneeshaw & Bergeron 1998, Pham *et al.* 2004). Two criteria were used for gap definition. In northern Fennoscandian conifer stands, interstitial space between crowns can be important, therefore, the opening had to result from the mortality of at least one tree. Also, regeneration within the gap had to be lower than two thirds of the height of the surrounding dominant trees (Kneeshaw & Bergeron 1998, Pham *et al.* 2004).



Fig. 1. Location of the study sites in the Pallas-Yllästunturi National Park, Lapland, Finland. The study area is in the northern Fennoscandian forest.

To estimate canopy gap fraction, total distance of the transect in canopy gaps was divided by total transect length. Gap size was assessed by measuring the longest axis and its perpendicular (dividing the first one in two equal parts). The ellipsoid formula was then used to obtain gap size (Runkle 1985a, 1992). Measurements were taken to the nearest 0.1 m with a Vertex device (Haglöf, Langsele, Sweden).

A gapmaker was defined as a dead tree with a DBH greater than 9 cm that contributed to gap formation (Runkle 1985a, 1992, Pham *et al.* 2004). We inventoried all gapmakers in every gap to obtain the following information: species, diameter at breast height (DBH), state of mortality (standing, snapped or uprooted), and orientation of downed boles for both snapped and uprooted trees. State of mortality referred to how the gapmaker was observed in the field. All dead trees (standing or down) were assigned to one of five decay states adapted from Hunter (1990):

early to recently dead: bark intact, small twigs and big branches remain, red to brown foliage can remain and wood is hard;

early to intermediate: bark partly intact, some small twigs might remain, big branches present, no foliage present and wood is hard;

intermediate: bark partly intact, small twigs absent, big branches present, softening of the wood;

intermediate to advanced: bark mostly gone, big branches more or less intact, wood is soft and breaks down in big chunks, the shape of the log is still round;

advanced: often without bark, big branches gone, wood is soft and breaks down into small chunks, the trunk has lost its round shape.

Radial cross-sections (disks) were taken from one to three gapmakers per gap. In some cases, it was impossible to sample any gapmakers because their state of decay was too advanced for dendrochronological analysis. Ideally, some of the bark had to remain attached to the sample disk as the outermost ring was used to determine the minimal year of mortality, and thus the year of gap creation. Samples were taken at different heights along each bole according to the state of decay of the gapmaker being sampled. A total of 112 trees, 94 *P. abies*, 8 *P. sylvestris* and 10 *B. pubescens*, were sampled.

Finally, to estimate tree composition and structure at each site, we used data sampled on the spatial variation of standing dead trees (T. Aakala unpubl. data). We measured both height (Vertex device) and DBH (to the nearest 1 cm) by species for all living and dead standing trees (> 9 cm DBH) within a 400 m × 40 m plot. Laasasenaho's (1982) taper equations were used to calculate volumes for *P. abies*, *B. pubescens* and *P. sylvestris*. Wood volumes for the other species were not calculated as they represented less than 2% of all trees in the area.

Dendrochronological analyses

Disks were sanded to even out the surface and two radii, based on the absence of reaction wood and the presence of bark at the edge of the disk, were traced and carved onto the disk with a razor blade. Water and magnesium powder were added to the carved radii to better expose the cells under the microscope. For each radius, annual rings were counted and measured to the nearest 0.01 mm using a sliding stage table interface linked to a computer.

Assessment of the year of tree death was done by cross-dating using the computer program COFECHA (Holmes 1983, Grissino-Mayer 2001). Trees may not produce complete rings for a given year as senescent trees may stop forming rings a few years prior to the cessation of leaf production (Mast & Veblen 1994, Cherubini *et al.* 2002); two radii thus provide a more accurate approximation of year of mortality as it reduces the risk of underestimation due to incomplete rings on part of the disk. In the case of a discrepancy between counts for the two radii, the most recent year was selected as the year of death. In our case, a master chronology already existed for both *P. abies* and *P. sylvestris* in the study region (M. Timonen & H. Herva pers. comm.). However, we only used the *P. abies* data, because too few *P. sylvestris* and *B. pubescens* were sampled to be considered representative.

A graphical visual verification was done by plotting the two radii tree-ring series against the master chronology with characteristic years (pointer years), i.e. 1902, 1928, 1931, 1948–1951 and 1981–1983, which were narrow rings (pers. obs.; Mäkinen *et al.* 2000), to verify whether tree-ring series followed a similar growth trend.

Growth release analysis

Growth release analyses were performed for all the *P. abies* gapmakers (94) sampled. We used the percentage-increase method proposed by Nowacki and Abrams (1997) to detect growth releases. Percentage growth change was calculated according to the following formula:

$$[(M_2 - M_1)/M_1] \times 100,$$

where M_1 is the average radial growth in the 10 preceding years (including the evaluated year), and M_2 equals the average radial growth in the 10 succeeding years. A 10-year running mean is commonly used because it filters out tree-ring response to short-term climatic changes (Lorimer & Frelich 1989, Nowacki & Abrams 1997, Black & Abrams 2003, 2004). Growth releases were then assessed based on the boundary line method developed by Black and Abrams (2004), where maximal potential releases are

dependent on prior growth rate. To do so, prior growth and percentage growth change were plotted by species for each ring of all measured trees. A boundary line was constructed by dividing the data set into 0.5-mm segments of prior growth and then averaging the top 10% growth change values for each segment.

A major growth release was considered to be a percentage growth increase greater than half (50%) of the maximum potential response (given by the boundary line) for a given previous growth (Black & Abrams 2004). All major growth changes recorded were then compiled by year of occurrence in order to establish the growth release time period distribution.

Statistical analysis

The distribution pattern of the gapmaker's state of decay, the temporal distribution pattern of gap timing, and the orientation pattern of the downed boles were tested with a chi-square test. Two-way contingency tables were used to verify whether the state of mortality interacted with decay stage and tree species. The number of gapmakers was also correlated with gap size (Pearson correlation, r).

The pattern of gap creation time (regular/irregular) was examined using a chi-square test with a one-way contingency table and was restricted to gapmakers that died after 1965, because prior to this year there were too few data.

The gap rotation, which corresponds to the amount of time needed to disturb an area equivalent to the one under study (Frelich 2002), was calculated using a truncated distribution of time since gap creation. This analysis was derived from the truncated time since fire analysis of Johnson and Gutsell (1994) and allowed us to consider all gaps, even those for which the year of creation could not be estimated. A truncated distribution of time since gap creation is done based on the time since the first observable opening could be identified in a transect. This corresponds to the age of the oldest cross-dated gap and all the undated gaps are assigned the age of the oldest cross-dated gap. The parameter b gives the gap creation period in years as a negative exponential distribution. Gap creation was

calculated on a transect base using the following equation:

$$b = \frac{ax' + \sum_{i=1}^r b_i x_i}{N}, \quad (1)$$

where x' is the age of the first observable opening by a the length of the transect in closed canopy, x_i is the time since gap i was formed and b_i the length of the transect intersecting gap i , r is the total number of aged gaps recorded, and N is the total transect length in gap.

Results

Stand characteristics

With all transects pooled, the structural characteristics of living trees revealed a mean density of 457.0 ± 51.8 trees ha^{-1} , a basal area of 15.5 ± 2.3 m^2 ha^{-1} and a volume of 104.2 ± 15.8 m^3 ha^{-1} (Table 1). Standing dead trees had a mean density of 94.1 ± 15.5 , a basal area of 5.0 ± 2.1 m^2 ha^{-1} and a volume of 14.5 ± 2.6 m^3 ha^{-1} . Based on the number of living trees, *P. abies* was the dominant species, followed by *B. pubescens* and a few *P. Sylvestris* among the remaining individuals (Table 1). In general, the proportion of living *P. abies* versus living *B. pubescens* was higher than the proportion of dead *P. abies* versus dead *B. pubescens*. These stand characteristics reflect the structure of *P. abies*-dominated forest sites.

Gap and gapmaker attributes

A total of 126 gaps were sampled along the 2400 m of transect investigated, which is roughly equivalent to one gap every 19 m (Table 2). We also observed two openings with no gapmaker. The total proportion of the forest area that was in gaps varied from 32% to 50%, with an average of $43.1\% \pm 7.5\%$ (SD) (Table 2). Gap sizes ranged from 25 m^2 to 1600 m^2 (Fig. 2); the average gap size was 221 ± 198 m^2 (SD) and the median gap size about 170 m^2 . The presence of two gaps greater than 1000 m^2 increased the average gap size considerably. While only 20% of the gaps were smaller than 100 m^2 , nearly 85% of them were smaller than 300 m^2 (Table 2).

In total, 556 gapmaker trees were inventoried, which is equivalent to 4.3 gapmakers per gap, with less than 4% of the gaps having more than 10 gapmakers and one gap having 20 gapmakers. There was a positive correlation between gap size and the number of gapmakers (Pearson $r = 0.46252$, $n = 127$, $p < 0.0001$).

Gapmaker trees were mostly composed of *P. abies* (72%), while *B. pubescens* accounted for 21% and *P. sylvestris* 4% of standing dead trees (Table 3). The state of mortality was significantly different among species ($\chi^2 = 32.49$, $df = 4$, $p < 0.0001$). Both *P. abies* and *B. pubescens* were commonly found snapped (74% and 89%,

respectively), while only 39% of dead *P. sylvestris* were snapped, 11% were standing and 50% were uprooted.

Dead trees were unequally distributed across the five decay stages ($\chi^2 = 274.65$, $df = 4$, $p < 0.0001$). For instance, around 40% of the gapmaker trees were in an advanced decay stage, while less than 10% of them were in an early to intermediate or early decay stage. There was a significant difference in the frequency of occurrence of decay stages in relation to the state of mortality ($\chi^2 = 86.74$, $df = 8$, $p < 0.0001$); in particular, the number and proportion of snapped trees increased with advancing stages of decomposition.

Table 1. Density, basal area ($\text{m}^2 \text{ha}^{-1}$), volume ($\text{m}^3 \text{ha}^{-1}$) and species proportion (spruce, birch and others) of living and standing dead trees for the six old-growth *Picea abies* study sites ($400 \text{ m} \times 40 \text{ m}$). Both living and dead trees refer to stems $> 9 \text{ cm}$ DBH.

Transect	Density (tree ha^{-1})	Basal area ($\text{m}^2 \text{ha}^{-1}$)	Volume ($\text{m}^3 \text{ha}^{-1}$)	Species proportion (%)*		
				Spruce	Birch	Others
Living trees						
1	516.9	15.5	100.8	66.0	33.3	0.7
2	472.5	15.0	104.2	63.5	35.2	1.3
3	490.0	13.9	90.9	64.0	35.2	0.8
4	446.3	12.9	84.6	57.0	37.8	5.3
5	365.6	19.4	125.5	79.3	20.2	0.5
6	450.6	16.7	119.3	77.7	15.8	6.5
Average \pm SD	457.0 \pm 51.8	15.5 \pm 2.3	104.2 \pm 15.8	67.4 \pm 8.7	30.0 \pm 9.2	2.5 \pm 2.7
Dead trees						
1	112.5	4.9	14.7	52.2	46.7	1.1
2	98.8	5.1	18.5	61.0	30.2	8.8
3	102.5	9.0	15.6	44.5	54.9	0.6
4	98.8	4.0	15.1	60.1	24.7	15.2
5	82.5	4.0	12.2	47.7	52.3	0.0
6	69.8	2.8	12.0	52.3	42.3	5.4
Average \pm SD	94.1 \pm 15.5	5.0 \pm 2.1	14.5 \pm 2.6	53.0 \pm 6.6	42.8 \pm 12.1	5.2 \pm 6.0

*Proportions are given based on tree density

Table 2. Gap descriptors presented by transect (1 to 6), mean and standard deviation (when applicable). The gap descriptors are canopy fraction (m), mean gap size (m^2), median gap size (m^2), range of gap size, % gaps $< 100 \text{ m}^2$, % gaps $< 300 \text{ m}^2$ and number of gaps.

Gap descriptors	Transect						Average	SD
	1	2	3	4	5	6		
Canopy gap fraction (%)	48.9	32.0	35.8	44.1	47.7	50.0	43.1	7.5
Mean gap size (m^2)	153.7	164.8	235.5	254.5	237.2	294.8	221.0	198.0
Median gap size (m^2)	113.3	162.2	170.2	202.2	203.6	249.5	170.2	
Range gap size	25–514	49–401	70–693	75–1599	55–855	91–1060	25–1599	
Gaps $< 100 \text{ m}^2$ (%)	39.1	20.0	19.1	9.1	13.6	5.3	17.7	11.9
Gaps $< 300 \text{ m}^2$ (%)	88.7	95.0	76.2	90.9	77.3	79.2	84.4	7.9
Number of gaps	97	68	80	102	93	116	92.7	16.8

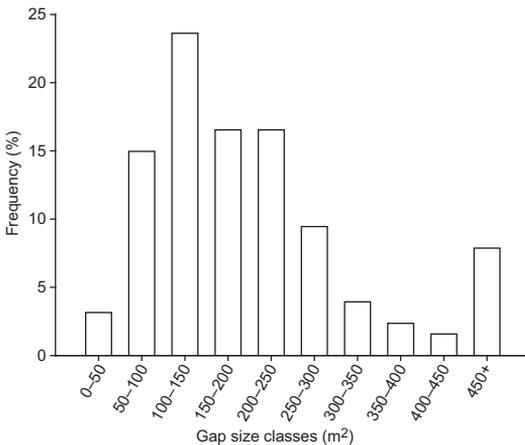


Fig. 2. Canopy gap size frequency distribution for all sites pooled together.

The orientation of downed boles was significantly different among the four directions tested (northwest, northeast, southeast and southwest; $\chi^2 = 91.21$, $df = 3$, $p < 0.0001$). The two dominant tree fall directions were northeast (30%) and southeast (40%), while the direction of the prevailing regional wind is southwest.

Temporal pattern of gap

Recent gap

We dated 59 gaps, which is slightly less than half of the total number of inventoried gaps. The other gaps could not be dated since gapmakers were too decayed for dendrochronological analysis and two gaps had no gapmakers. The youngest gap was created in 2005 (the survey year) and the oldest one in 1922, and 75% were younger than 40 years, i.e. created after 1965 (Fig. 3).

Gap creation in 5-year time windows for the 1965–2005 period was irregularly distributed (χ^2

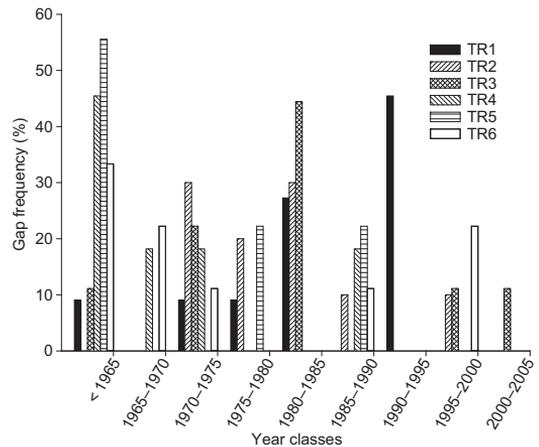


Fig. 3. Frequency distribution of canopy gaps having formed after 1965, according to their period of creation (divided into 5-year classes) by transect (TR1: $n = 11$ gaps; TR2: $n = 10$; TR3: $n = 9$; TR4: $n = 11$; TR5: $n = 9$; TR6: $n = 9$).

$= 21.08$, $df = 8$, $p = 0.007$) (Fig. 3). There were no peaks in gap creation that occurred simultaneously across the entire study area. Years of gap creation were highly variable from one transect to another, and no general trend was observed (Fig. 3). The estimated gap rotation varied between 174 to 334 years among transects, with an average of 248 ± 56 (SD) years for the whole study area (Table 4). This means that it would take approximately 250 years to have an area equivalent to our study area entirely affected by gap disturbance.

Growth release and disturbance reconstruction

Growth releases were dated as early as 1690 (Fig. 4). In 72% of the sampled trees, at least one major growth release was recorded. The time dis-

Table 3. Number of gapmakers identified as snapped, standing and uprooted according to species. The number in parenthesis corresponds to the percentage of standing, snapped and uprooted gapmakers for a given species.

	Snapped	Standing	Uprooted	Total
<i>Picea abies</i>	300 (74%)	29 (7%)	76 (19%)	405
<i>Betula pubescens</i>	117 (89%)	5 (4%)	9 (7%)	131
<i>Pinus sylvestris</i>	7 (39%)	2 (11%)	9 (50%)	18
Others	0	2 (100%)	0	2

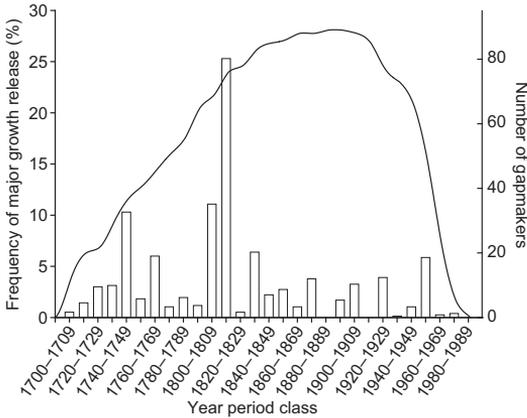


Fig. 4. Frequency of major growth releases for gapmakers by 10-year class (as represented by the bar distribution). The line distribution represents the number of gapmakers that were sampled (the right-hand-side y-axis) by 10-year classes.

tribution of major growth releases was irregular and decades with a high number of releases were observed (Fig. 4). For instance, the periods 1810–1819 and 1820–1829 had the highest proportion of trees showing a major growth release. Furthermore, the number of major growth releases was highest in the decade 1820–1829. The 1810–1819 period also stood out, but to a lesser extent. Thus, two episodes with a high number of past major growth releases were found in the study area.

Discussion

Canopy and gap characteristics

The studied old-growth *P. abies* stands had a more open canopy (average area in gaps: 43%)

than what has been reported in some previous studies in pristine boreal spruce forests. For example, Liu and Hytteborn (1991) in central Sweden and Drobyshev (1999) in Russia's southern taiga estimated that 31% and 35% of total forest area, respectively, was in gaps. Gap sizes were also larger than previously reported, with most of the gaps being bigger than 100 m². In studies by Drobyshev (1999), Liu and Hytteborn (1991) and Leemans (1991), most of the gaps were smaller than 100 m². In fact, the median gap size in our study was about two times greater than the average size reported for *P. abies*-dominated stands in central Sweden (Liu & Hytteborn 1991). These larger gap sizes were observed despite the fact that our gaps were created by the death of 2–5 trees as compared with the range of 1–10 gapmakers per gap reported by Liu and Hytteborn (1991). The northern location of our study sites may be the reason for the observed discrepancies with studies carried out in more southern locations since the northern sites have lower site productivity, lower tree density and slower gap filling, thus resulting in larger gaps (Sirén 1955).

Gap dynamics

As hypothesized, the old-growth *P. abies* stands studied had no distinct peaks in gap creation during 1965–2005. Gap creation occurred constantly, albeit irregularly. The observed 'quasi-constant' gap creation pattern in old-growth *P. abies*-dominated stands suggests a quasi-equilibrium stand structure (Shugart 1984). This result agrees with previous views proposing that the

Table 4. Length of transect in gap (m), canopy gap fraction, time since initial gap creation, and estimated gap rotation by site and as an average for the entire study area. The length of each transect was 400 m.

Transect	Length of transect in gap (m)	Length of transect in a dated gaps (m)	Oldest gap (years)	Rotation (years)
1	195.4	96.3	59	209.0
2	127.9	70.9	32	173.6
3	143.1	63.6	48	277.3
4	176.4	81.1	74	333.6
5	190.6	111.8	83	260.5
6	200.0	99.8	67	234.9
Average ± SD	172.2 ± 27.3	87.3 ± 16.9	60.5 ± 16.9	248.2 ± 55.8

development and maintenance of old pristine *P. abies* forests is mainly driven by endogenous small-scale disturbances (Norokorpi 1979, Kuuluvainen *et al.* 1998, Edman *et al.* 2007, Fraver *et al.* 2008). No temporal synchronicity in gap creation that could be associated with larger-scale exogenous disturbances was detected among the sites. Also, the presence of different decay classes further suggests that gap creation was not due to a single event, but rather to a continuous series of small-scale mortality events. Similar old-growth *Picea* forest dynamics were documented by Fraver *et al.* (2008) in boreal Sweden.

With increasing age, *P. abies* is more likely to be affected by heart rot (Norokorpi 1979), which weakens the tree and then makes it more sensitive to exogenous disturbances such as strong winds or heavy snow loads (Kuuluvainen 1994, Fraver *et al.* 2008, Länneppää *et al.* 2008). Liu and Hytteborn (1991) and Fraver *et al.* (2008) found that wind plays a role as the final cause of treefall, and Jonsson and Dynesius (1993) noted that the direction of tree fall of uprooted trees corresponded with predominant wind direction. However, in our study, other causes of treefall may be involved as 30% of the trees fell north-easterly, which is along the axis of the dominant winds. The strong northwestern wind observed in eastern Lapland (H. Kauhanen pers. comm.) may support the fact that 40% of the fell south-westerly. Thus, our results suggest that both the predominant wind and the strongest wind influence the final cause of treefall.

The long gap rotation of nearly 250 years is most probably a consequence of the absence of cyclical moderate-severity disturbances and the longevity of *P. abies*. Our study thus supports the occurrence of long fire-free periods in the Scandinavian boreal forest (Hofgaard 1993, Hörnberg *et al.* 1995, Kuuluvainen *et al.* 1998, Wallenius *et al.* 2005). Besides the absence of fire, the absence of insect outbreaks evidently contributes to the long gap rotation. In eastern Quebec, Pérignon (2006) derived a much shorter rotation ranging from 60 to 105 years in *Picea mariana* and *Abies balsamea* stands, while Kneeshaw and Bergeron (1998) obtained estimates similar to ours for the boreal forest of western Quebec.

Tree longevity may play an important role in that region. For instance, both *P. mariana* and *A. balsamea* have a lifespan of 100–200 years (Burns & Honkala 1990) while *P. abies* lives up to 410 years (Hofgaard 1993).

Do large-scale disturbances play a role?

The results of our growth release analysis suggest that larger disturbances may also have taken place farther back in time. Also, in the study of Fraver *et al.* (2008), it was concluded that *P. abies* forest development is generally slow but punctuated with moderate-severity disturbances. Over the two centuries covered in our study, the decades 1810–1819 and 1820–1829 recorded the highest frequency of trees experiencing major growth releases, with 11% and 25% of all sampled trees, respectively. These peaks were observed in both study areas and in all stands, which suggests an exogenous disturbance event common to all areas. Surface fires could be considered, as they reduce competition, are linked to climatic conditions, and are known to have been more frequent prior to the early 1800s in Fennoscandia (Zackrisson 1977, Linder *et al.* 1997, Wallenius *et al.* 2005).

Whatever the cause behind the higher frequency of growth releases, the results suggest that *P. abies*-dominated stands may also be on occasion subject to larger-scale disturbances, which are not stand-replacing. However, because the intervals between large-scale disturbances is obviously very long (hundreds of years), in late-successional stages, the pristine spruce forests become characterized by more or less continuous endogenous small-scale gap disturbances, resulting in quasi-equilibrium landscapes that maintain their structure until the next large-scale disturbance event. This view is in accordance with some earlier results and views on pristine *P. abies* forest dynamics (e.g. Sernander 1936, Syrjänen *et al.* 1994, Kuuluvainen *et al.* 1998, Gromtsev 2002). However, after severe large-scale disturbances, the successional time needed before this quasi-equilibrium state emerges in northern *Picea* forests can be substantial, i.e. up to 300 years (Lilja *et al.* 2006).

Conclusion and management implications

The studied pristine old *P. abies* forests in northern Fennoscandia were driven by continuous small-scale disturbances and were characterized by quasi-equilibrium structure and dynamics. However, we also found some evidence of past large-scale disturbance(s) that may have triggered a period of non-equilibrium forest dynamics. Emulating this type of forest dynamics for habitat and biodiversity conservation in forest management would imply selective or group harvesting of trees as the predominant methods, but larger-scale, more intensive cuttings could also be carried out periodically.

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